

Communities in Neuronal Complex Networks Revealed by Activation Patterns

Luciano da Fontoura Costa

*Institute of Physics at São Carlos, University of São Paulo,
PO Box 369, São Carlos, São Paulo, 13560-970 Brazil*

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Recently, it has been shown that the communities in neuronal networks of the integrate-and-fire type can be identified by considering patterns containing the beginning times for each cell to receive the first non-zero activation. The received activity was integrated in order to facilitate the spiking of each neuron and to constrain the activation inside the communities, but no time decay of such activation was considered. The present article shows that, by taking into account exponential decays of the stored activation, it is possible to identify the communities also in terms of the patterns of activation along the initial steps of the transient dynamics. The potential of this method is illustrated with respect to complex neuronal networks involving four communities, each of a different type (Erdős-Rényi, Barabási-Albert, Watts-Strogatz as well as a simple geographical model). Though the consideration of activation decay has been found to enhance the communities separation, too intense decays tend to yield less discrimination.

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*‘Zora’s secret lies in the way your gaze runs over patterns following one another as in a musical score...’ (I. Calvino, *Invisible Cities*)*

I. INTRODUCTION

Neuronal networks (e.g. [1, 2, 3]) and complex networks (e.g. [4, 5, 6, 7]) can be understood as sister research areas. However, as the latter is much younger (especially regarding the developments from 1999), these two sisters have yet to get fully acquainted one another. Such a natural integration has already begun (e.g. [8, 9, 10, 11, 12, 13, 14, 15, 16]) and is poised to continue to the point that these two areas become not only close relatives, but also best friends. This integration is particularly interesting for both neuronal networks and complex networks because of the complementation of the approaches which have been respectively adopted. More specifically, while neuronal networks have relied strongly on pattern recognition and dynamical systems, complex networks have been strongly focusing on structure, with a recent surge of interest on dynamics (e.g. [5, 17]). However, as special emphasis has been placed on the important problem of linear synchronization (e.g. [17]), few works have addressed non-linear or transient dynamics (e.g. [18, 19]). In complex networks, emphasis has been placed on the modularity of the connections or community structure (e.g. [20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31]), which has important implications for both the structure and dynamics of networks. The integration between neuronal networks and complex networks is henceforth referred to as *complex neuronal networks*, which has special importance for non-linear dynamical systems underlain by structured and complex connectivity.

Recently [32, 33], complex neuronal networks involving simple integrate-and-fire neurons (each neuron is repre-

sented as a node) have been studied with respect to their transient dynamics. Figure 1 illustrates the type of neuronal cell adopted in those works. The incoming activation, received through the $n(i)$ dendrites, is integrated and accumulated in the internal state $S(i)$ until its value exceeds the threshold $T(i)$, in which case the cell fires, liberating the accumulated activation between the $m(i)$ outgoing edges (axons). In the previous works [32, 33], in order to maintain the total received activation, which was fed through a single selected neuron, the accumulated activation $S(i)$ was uniformly distributed among the $m(i)$ outgoing connections, each therefore receiving a share of $S(i)/k_{out}(i)$, where $k_{out}(i) = m(i)$ is the out-degree of node i .

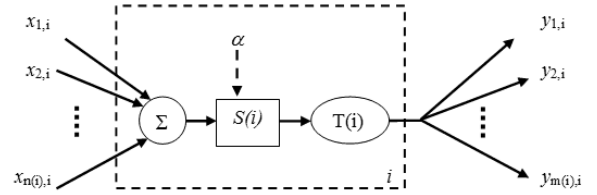


FIG. 1: The integrate-and-fire neuronal cell adopted in the previous works [32, 33] incorporates three stages: (i) integrating of input activations; (ii) memory of activation $S(i)$; and (iii) non-linear transfer function involving a threshold $T(i)$ (a hard limiter). While those previous works adopted full conservation of the activation (i.e. decay rate $\alpha = 0$), in the present work the stored activation undergoes exponential time decay with rate α .

Several interesting dynamic features are implied by such a simple neuronal model. First, the accumulation of the received activity is related to the important phenomenon of *facilitation* of firing. Roughly speaking, the

income of a spike into a cell enhances the probability of its future spiking by occasion of subsequent activations. Second, the non-linear element implies the activation to remain stored until the threshold is reached, which contributes strongly to constraining the activation locally in the network along topology and time. As all neurons are henceforth assumed to have the same threshold $T = 1$ (a biologically reasonable choice), the distribution of outgoing activation implied by each spiking becomes imperative in order not to yield one spike at every time step. Similar effects can be obtained by associating weights smaller or equal to one to each edge (synaptic weight). The combination of such non-linear effects has been observed [33] to contribute decisively for constraining, along a transient period of time, the activation inside the community which contains the source of activation. Such an effect allows the identification of neuronal communities by considering the transient non-linear dynamics in the whole network while it is stimulated by sources of activations placed at each of its neurons. It has been experimentally verified that the time it takes for each cell to receive non-zero activation in any of its dendrites, called the *beginning activation time* of each cell, seems to be particularly relevant for the identification of the communities. Promising results were obtained with respect to two synthetic (networks including 3 and 4 communities with uniform connectivity) as well as a real-world network (*C. elegans* [20]).

However, the previous investigations reported in [33] considered no time decay of the stored activation $S(i)$, which seems to have been responsible for making the beginning activation times decisive for the proper identification of the communities. In the present work we consider the more biologically realistic situation involving exponential decays of the activations. More specifically, at each time step each stored activation is decreased at a constant rate α , i.e.

$$S^{t+1}(i) = S^t(i) - \alpha S^t(i) \quad (1)$$

where t is the time step and $0 \leq \alpha < 1$.

The net effect of the decay is to generally delay the firing of cells. Interestingly, such an effect seems to allow proper identification of the communities also by considering the average activation of the network along an interval of the transient dynamics, instead of only the beginning activation time. This is possibly a consequence of the fact of the enlarged period of time required to convey the activation from one community to another, which is enhanced by the decays. This possibility is experimentally investigated in the current article by considering hybrid networks containing four communities of different types (Erdős-Rényi, Barabási-Albert, Watts-Strogatz as well as a simple geographical model). Several combinations of inter and intra-community intensities of connections are considered. The activation is averaged from the beginning of the source operation for a total of H steps along the transient dynamics. Then, the statis-

tical method known as Principal Component Analysis (PCA) is applied to the activation patterns in order to reduce their dimensionality, which is optimally obtained by decorrelation of the activation. The original communities could be properly detected in most cases, even for the Barabási-Albert and geographical models. Combined with the investigations reported previously [33], the results obtained in the current work substantiate further the importance of the transient regime for characterization of modularity regarding both structure and dynamics in complex systems. With respect to the specific area of neuronal networks, the relationships between structured connectivity, in the form of communities, and the activation and spiking dynamics provide several implications for synchronization, pattern recognition and memory. The proposed methodologies may also prove useful as practical methods for identification of communities in more general types of networks.

The current article starts by presenting the basic concepts in complex neuronal networks, the four adopted theoretical models of complex networks, and the statistical method of Principal Component Analysis. The results, discussion, and perspectives for future works are presented subsequently.

II. BASIC CONCEPTS

A directed, unweighted network Γ can be completely specified in terms of its *adjacency matrix* K . Each edge extending from node i to node j is represented $K(j, i) = 1$. The absence of connection between nodes i and j implies $K(j, i) = 0$. The nodes which receive a direct edge from a node i are called the *immediate neighbors* of i . The *out-degree* of a node i is equal to the number of its immediate neighbors.

Four theoretical models of complex networks (e.g. [4, 5, 6, 7]) have been used in order to construct the hybrid community networks considered in this work: Erdős-Rényi (ER), Barabási-Albert (BA), Watts-Strogatz (WS) as well as a simple geographical type of network (GG). An Erdős-Rényi network (see also [34]) can be obtained by establishing connections between pairs of nodes with constant probability. The BA networks were obtained by starting with m_0 nodes and progressively incorporating new nodes with m edges, which are attached to the remainder nodes with probability proportional to their respective degrees. The WS structures were obtained by starting with a linear regular network of suitable degree and subsequently rewiring 10% of its edges. The geographical structures are obtained by distributing N nodes along a two-dimensional space and then connecting each pair of nodes whose distance does not exceed a given threshold. Though all these networks are *undirected*, we obtained the respective directed neuronal complex networks by considering the incoming on outgoing directions of each edge as dendrites and axons, respectively. Therefore, the so-obtained networks are directed

and have in-degree identical to the out-degree.

The *integrate-and-fire neuron* adopted in this work has been described and discussed in the Introduction. The activation and spiking of all neurons in the network can be represented in terms of diagrams which are henceforth called *activogram* and *spikegram*, respectively. These diagrams are matrices storing the transient activation or occurrence of spikes for every node. In this article, the activation of the network is always performed by injecting external activation of intensity 1 at each of the neurons. The time it takes for each neuron i , from the onset of the external initiation, to receive the first non-zero input is henceforth called its respective *beginning activation time* $T_a(i, v)$. The time it takes for that neuron to produce the first spike is the *beginning spiking time* $T_s(i, v)$.

Because the activation patterns obtained with the source in each of the N neurons involve N measurements, a highly dimensional space is implied. As a consequence of the intrinsic correlations between the activation patterns, it is possible to apply the PCA method to optimally decorrelate those patterns and yield meaningful 2D and 3D projections. Let each of the N observations $v = \{1, 2, \dots, N\}$ be characterized by the average activations of all nodes as a consequence of the activation source placed at node v . These measurements can be organized into respective *feature vectors* \vec{f}_v , with elements $f_v(i)$, $i \in \{1, 2, \dots, N\}$. Let the *covariance matrix* between each pair of measurements i and j be defined as

$$C(i, j) = \frac{1}{N-1} \sum_{v=1}^N (f_v(i) - \mu_i)(f_v(j) - \mu_j) \quad (2)$$

where μ_i is the average of $f_v(i)$ considering all the N observations (i.e. activations). The eigenvalues of C , sorted in decreasing order, are henceforth represented as λ_i , $i = 1, 2, \dots, M$, with respective eigenvectors \vec{v}_i . The matrix G given in Equation 3, obtained from the eigenvectors of the covariance matrix, defines the stochastic linear transformation known as the *Karhunen-Loève Transform* [7, 35].

$$G = \begin{bmatrix} \leftarrow & \vec{v}_1 & \rightarrow \\ \leftarrow & \vec{v}_2 & \rightarrow \\ \cdots & \cdots & \cdots \\ \leftarrow & \vec{v}_m & \rightarrow \end{bmatrix} \quad (3)$$

with $m = N$. Because such a transformation optimally decorrelates the activation patterns, concentrating the variance of the observations along the first axes (the so-called principal axes or variables), it is frequently possible to reduce the dimensionality of the measurements without substantial loss of information by considering the above matrix with $m \ll N$. The new, projected measurements \vec{g} , with dimension m , can now be straightforwardly obtained in terms of the following linear transformation

$$\vec{g} = G\vec{f}. \quad (4)$$

III. RESULTS AND DISCUSSION

Figure 2 illustrates the 9 networks adopted in the present investigation. Each of them involves 4 communities, of respective ER, BA, WS and GG types (see legend at the bottom of the figure) and approximately 50 nodes each. The intra-community degrees, expressed in terms of the BA parameter m , increase along the columns (top to bottom), and the inter-community degrees k increase along the rows (left to right). The considered values of intra- and inter-connectivity are shown in Figure 2. The same intra-connectivity degree, defined with respect to the parameter m of the BA model, was adopted for all the 4 communities in each case. The consideration of hybrid communities involving several network models is particularly useful for investigating the community detection methodology with respect to varying connectivity patterns.

Each network was searched for community structure by placing the activation source (with intensity 1) at each of its neurons and simulating the respective activation and spiking along the initial $H = 200$ steps of the transient dynamics. Three whole set of simulations were performed by considering respective decay rates α equal to 0.02 and 0.5. Figure 3 shows the activogram and spikegram, as well as the diagrams of beginning activation times and beginning spiking times for the network with $m = 3$, $k = 0.2$ and $\alpha = 0.02$.

The constant activation fed through neuron 25 is clearly identified as the white column in the activogram and spikegram. Because of the more intense interconnectivity between the nodes in the community to which this neuron belongs (ER, in this case) the propagation of activation and spikes tend to occur first inside this community, being propagated to the other communities only later. One exception are the neurons around node 125, which belong to the WS community. Because neuron 125 is connected to the ER community with particular intensity (more than one edge), it receives considerable activation sooner, leading to a progressive spreading of activation within the WS community. However, because this effect is not verified for most of the other nodes of the ER community, it tends to become less relevant in the subsequent decorrelation projection implemented by the PCA. In addition, except for a few other cells, the nodes which are inside the same community tend to receive activation relatively soon, as illustrated in the respective diagram of beginning activation times. A less regularly simultaneous activation is obtained for the spikes in the respective beginning spiking times diagram. The incorporation of suitable (not too large) values of decay seems to promote more stable activation patterns for the source placed at neurons of a same community as a consequence of further constraints on the dispersion of the activation. In this work we consider for the community identification the patterns of activation obtained by integrating the activation from time 0 to $H = 200$. Observe that the parameter H has important implications for the compu-

tational cost, in the sense that the larger its value, the larger the number of computations.

Figure 4 depicts the clusters obtained in the two-dimensional space defined by the first two PCA variables considering the average activation patterns and decay $\alpha = 0.02$. Figure 5 shows the respective scatterplots obtained for the first and third PCA variables. Therefore, it is possible to have a clear idea of the 3D PCA space by considering these two images. In these figures, as well as all the other subsequent ones, the original communities are identified by respective colors: ER in blue; BA in green; WS in red and GG in magenta. In most cases, especially for low ratios k/m , the original communities were mapped into well-defined respective clusters in the PCA space. For instance, in the case $m = 2$ and $k = 0.1$, we have dense clusters obtained for the ER and BA communities. Because of their intrinsic nature, the WS and GG models tended to yield larger dispersions in most of the cases considered in this work. Yet, they are well-separated, as it can be verified by considering both the $pca1 \times pca2$ (Figure 4) and $pca1 \times pca3$ (Figure 5) diagrams. Except for the WS case, the other 3 communities still tended to map to reasonably well-defined local regions in the PCA projections for larger values of intercommunity connection (i.e. $k = 0.5$ and 1). The separation between the community clusters tended to increase substantially from top to down along each column in Figures 4 and 5 as a consequence of the increase of the intra-community connectivity relatively to the intercommunity density of connections.

The PCA scatterplots obtained by considering more intense decay (i.e. $\alpha = 0.5$) are shown in Figures 6 and 7 respectively to the $pca1 \times pca2$ and $pca1 \times pca3$ projections. Less separated clusters have been obtained in most cases, with intense overlap between communities. However, the nodes belonging to the original communities still tended to be mapped to nearby positions in the scatterplots. Such a decrease in the community identification is a direct consequence of the fact that more intense decays tended to produce less stable activation patterns for the activation source placed at different nodes. In addition, the consideration of more intense decay also would imply in averaging the activations along a longer period of time, demanding additional computations.

IV. CONCLUDING REMARKS

In continuation to recent previous investigations [33], the relationship between topological and dynamical modularity during the transient period of activation of non-linear integrate-and-fire complex neuronal networks has been explored further, with respect to the consideration of average activation patterns as resources for community identification. By increasing the latent period in which the activation has to increase until firing is reached in the neuronal cells, relatively small non-zero decays of the accumulated activation tended to allow the subsequent

identification of the topological communities as clusters appearing in scatterplots obtained by optimally decorrelated PCA projections.

Such a phenomenon has been experimentally investigated by considering several hybrid networks, with communities of different types, and varying ratios of intra- to intercommunity connectivity. In most cases the original communities were mapped onto adjacent sets of points (clusters) which were often well-defined and delimited. As in [33], the nodes at the interfaces between the obtained clusters tended to correspond to those nodes implementing the intercommunity connections. The ER and BA modules tended to produce more concentrated clusters, with the WS and GG communities often yielding scattered, but still separated, distributions in the PCA diagrams. The discrimination between the communities was undermined when a substantially large decay was considered. As observed previously [33], the transient confinement of the activation inside each community seems to be related to an abrupt pattern of activation observed for several models of complex networks [32]. As a matter of fact, the WS and GG models had indeed been observed [32] to produce less abrupt activations. The situations involving higher values of α would also imply substantially higher computational cost required for the simulation of the activation along longer transient periods. Nevertheless, it seems to follow from the currently reported results that relatively small non-zero decay of the accumulated activation, to a certain extent, emphasizes the transient confinement of activation inside the communities.

These findings substantiate the importance of transient dynamics for the characterization and analysis of non-linear complex systems. Furthermore, the relationship between modular interconnectivity and nearly simultaneous activation of communities has several implications for biological and computational neuroscience. In particular, such a relationship can be intrinsically related to recognition of patterns and associative memory. For instance, the nearly simultaneous activation of the communities could play an important role in reconstructing larger patterns (communities) from incomplete presentations. Because of the temporal dynamics of nervous systems, where problems have to be solved by functional modules of neurons along a given period of time (e.g. [36, 37]), it is possible that the phenomenon of simultaneous activation within communities plays an important general role in neuronal organization and functionality. The neuronal community identification methodology is also promising for the identification of functional modules in the cortex or neuronal subsystems because of its intrinsic compatibility with the non-linear dynamics performed in those systems.

Several are the future works implied by the results and methods reported in the current article. First, it would be important to perform more objective investigations of the discriminability between the PCA clusters, for instance by using the intra- and inter-class scatterings

(e.g. [35]) and comparing the results obtained for the synthetic hybrid communities with those yielded by canonical analysis (e.g. [7, 38]). It would also be necessary to consider larger ensemble of networks in order to reach more general and definitive conclusions regarding the effect of the few parameters involved (i.e. α and H), as well as concerning possible finite-size and scaling effects. Valuable insights about the influence of the connectivity on the transient non-linear dynamics of the complex neuronal networks considered in this work can be potentially achieved by applying the systematic approach of superedges [18]. Of particular interest are further investigations aimed at the characterization of the abrupt

activations verified for several complex network models. This phenomenon, which is possibly associated to phase transition and/or self-organized criticality, seems to lie at the heart of the confinement of the activation inside the communities during the transient activation.

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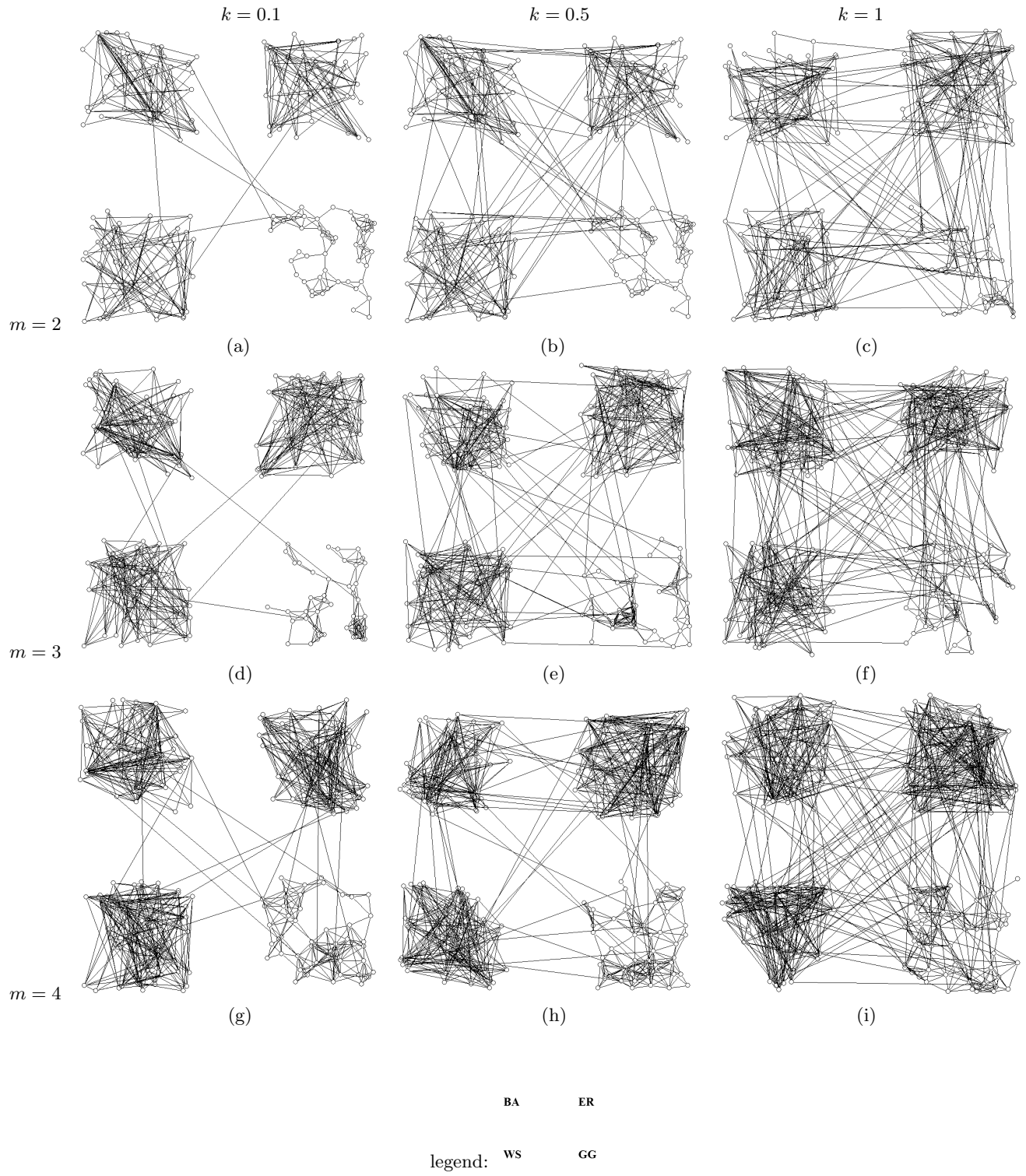


FIG. 2: The 9 hybrid networks considered in this work incorporate 4 communities each, of respective ER, BA, WS and GG types (see legend at the bottom).

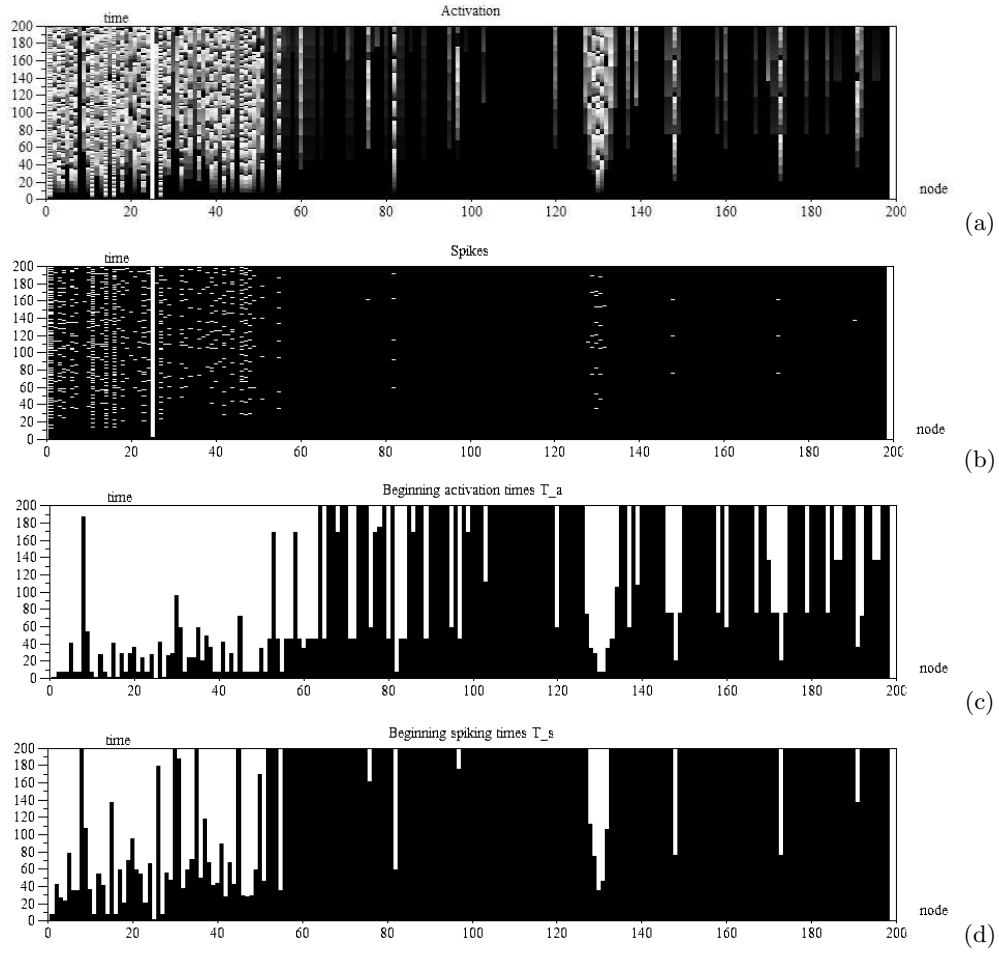


FIG. 3: The activogram and spikegram, as well as the diagrams of beginning activation times and beginning spiking times obtained for the 200 initial time steps with activation source at node 25 for the complex network with $m = 3$, $k = 0.5$ (Figure 2e) and $\alpha = 0.02$.

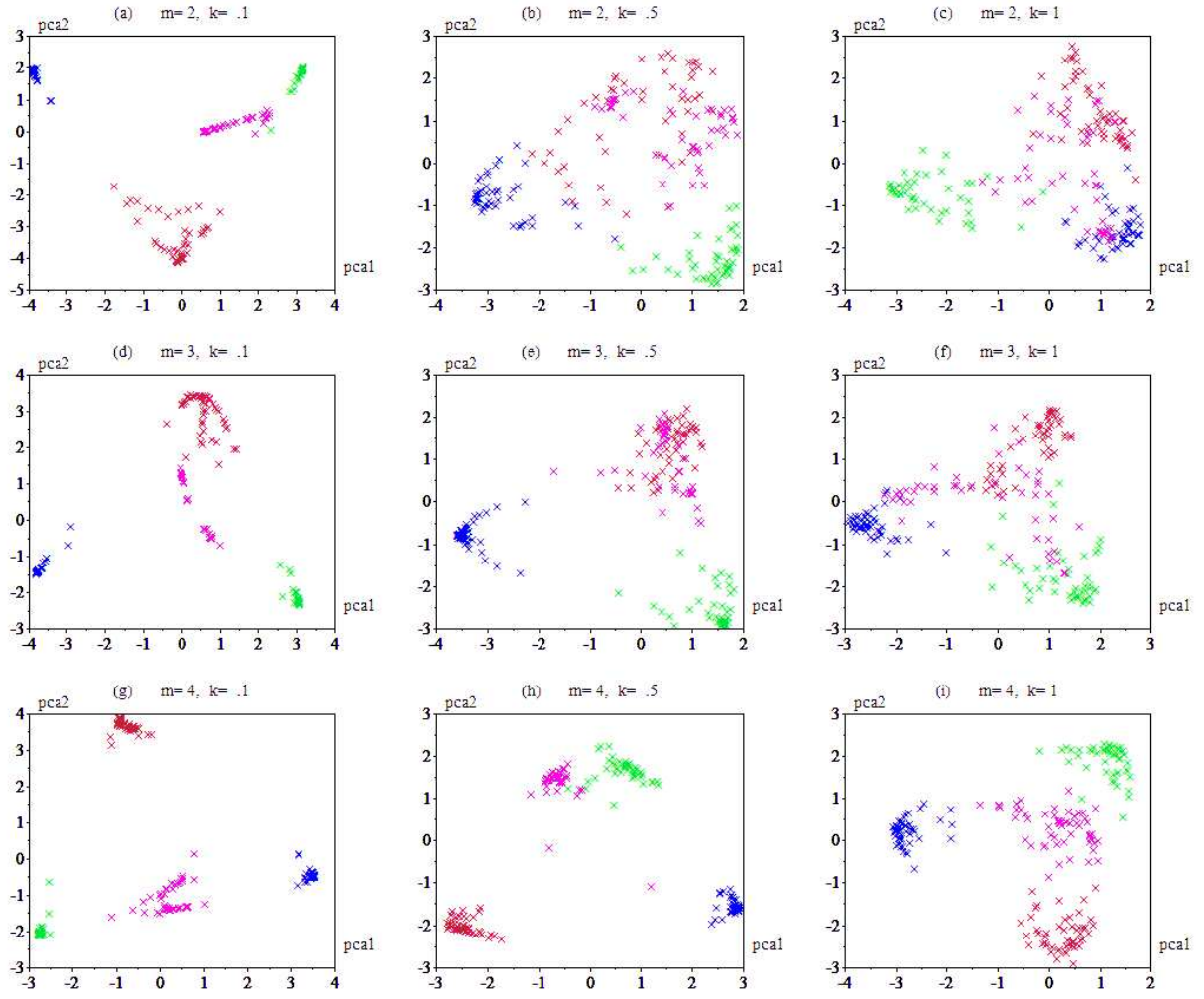


FIG. 4: The clusters obtained by considering the first and second PCA variables for $\alpha = 0.02$.

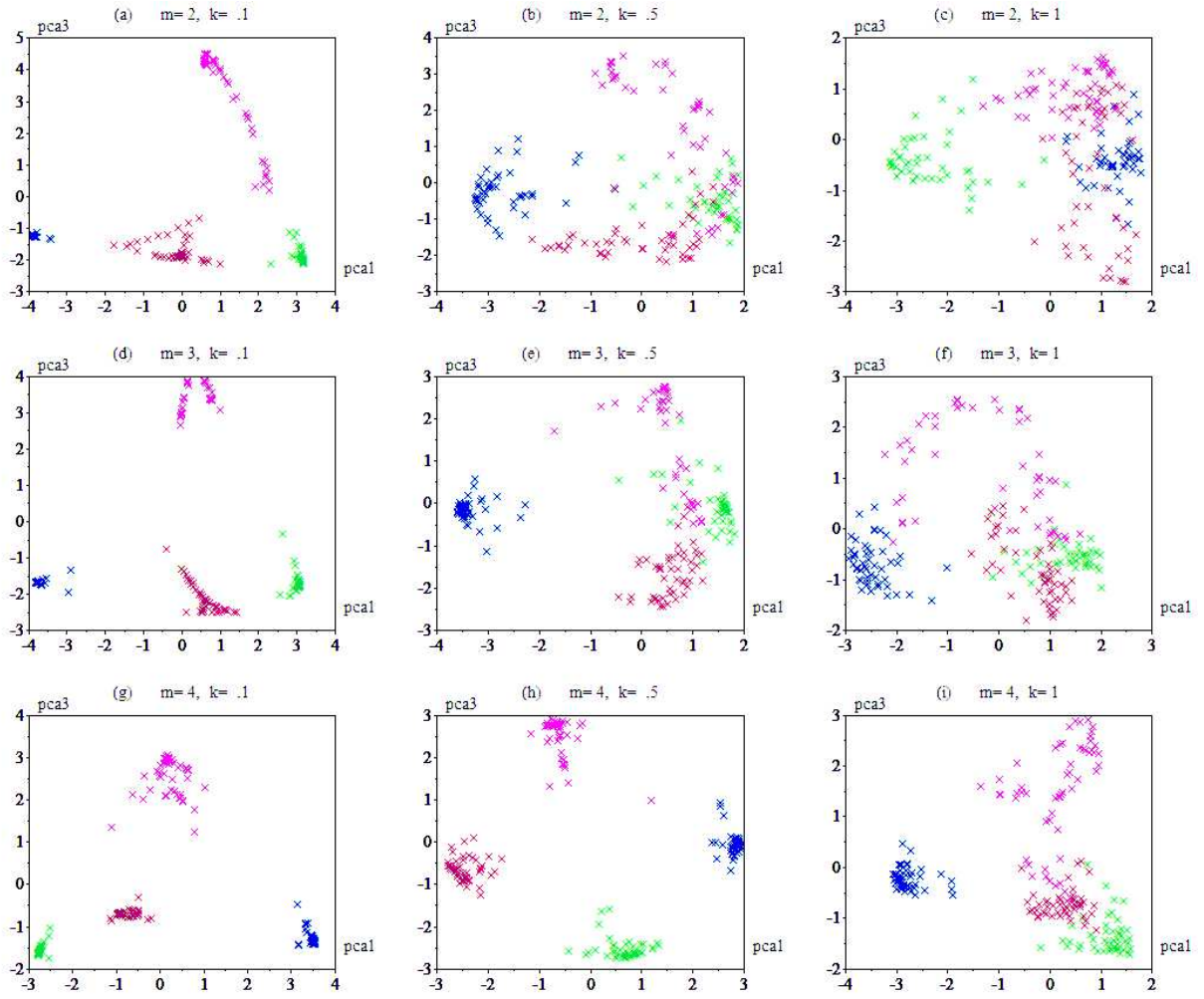


FIG. 5: The clusters obtained by considering the first and third PCA variables for $\alpha = 0.02$.

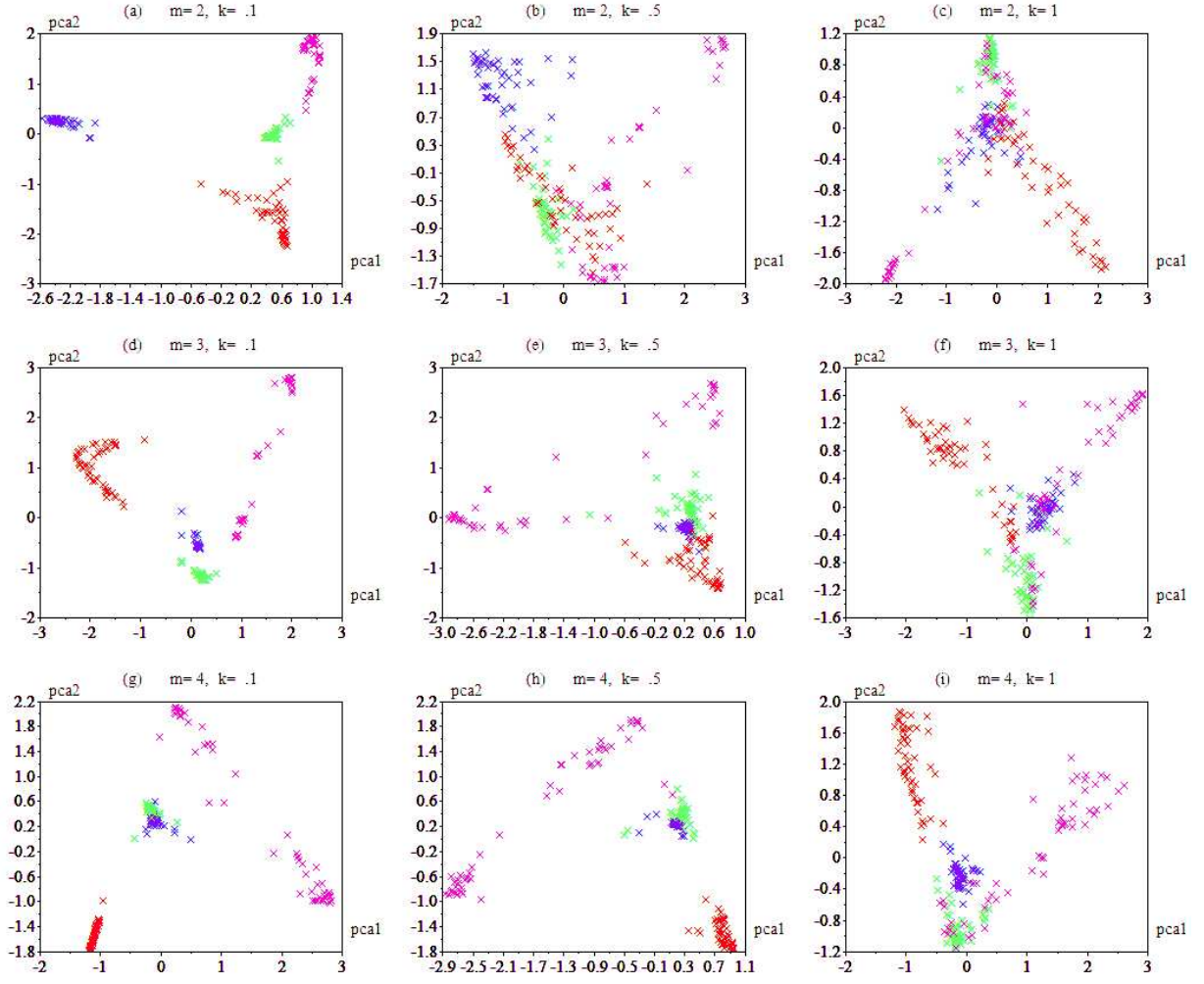


FIG. 6: The clusters obtained by considering the first and second PCA variables for $\alpha = 0.5$.

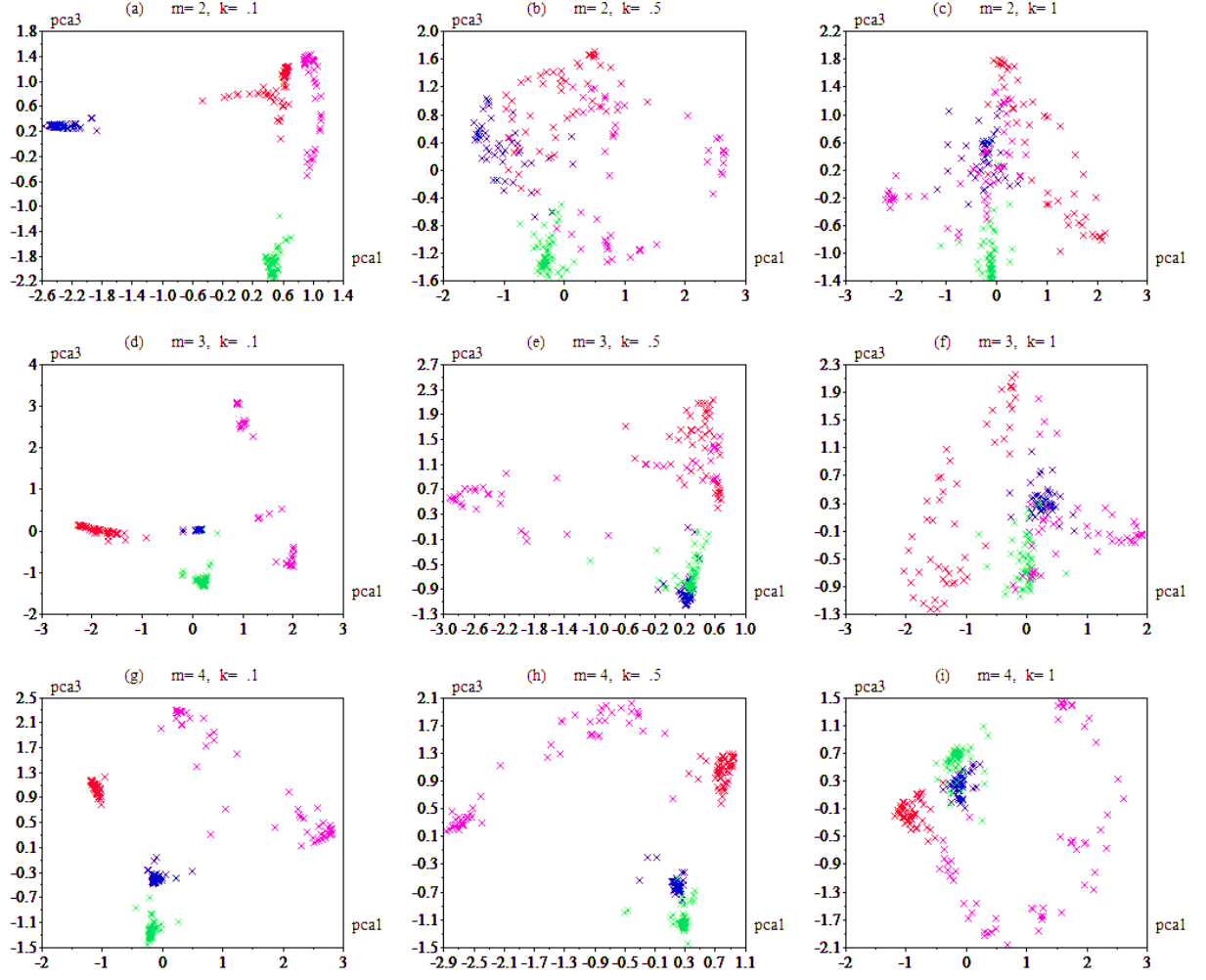


FIG. 7: The clusters obtained by considering the first and third PCA variables for $\alpha = 0.5$.